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REINSTATEMENT OF *TONESTUS* (ASTERACEAE: ASTEREAE)

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ABSTRACT

In order to provide a complete, formal nomenclature for the genus *Tonestus*, we propose the following new combinations: **T. aberrans** (A. Nels.) Nesom & Morgan, **T. alpinus** (L. Anderson & S. Goodrich) Nesom & Morgan, **T. graniticus** (Tiehm & Shultz) Nesom & Morgan, **T. microcephalus** (Cronq.) Nesom & Morgan and **T. peirsonii** (Keck) Nesom & Morgan. A generic description of *Tonestus* is presented, and the distinction between *Tonestus* and *Stenotus* is considered. With one exception and one qualification, the nomenclatural combinations in *Tonestus* also complete the apportionment of species of the polyphyletic North American *Haplopappus* (sensu Hall), among its constituent genera.

KEY WORDS: *Haplopappus, Tonestus*, Asteraceae, Astereae, North America.

In North America, the genus *Haplopappus* has encompassed a wide variety of species groups (Hall 1928), increasingly recognized in modern literature as phylogenetically disparate (Lane, *et al.* 1987). Although it is perhaps not universally agreed upon, we agree with Brown & Clark (1982) that *Haplopappus* sensu stricto is restricted to several sections that are endemic to South America. *Haplopappus* sect. *Polyphylla* of South America and the genus *Hazardia* of North America are closely similar and they may be congeneric. Except for *Hazardia*, however, none of the North American sections of *Haplopappus* sensu Hall can be considered to be congeneric with true *Haplopappus*.

The following synopsis provides an account of all sections of North American *Haplopappus* and their current taxonomic rank and/or placement. For those wishing to recognize the segregates of *Haplopappus*, the combinations are now available for all species involved, with the few exceptions noted below.

Sect. *Blepharodon* as part of *Machaeranthera* (Hartman 1976). Three species (the "phyllocephalus group") of sect. *Blepharodon* sensu Hall were said by Hartman (1976) to represent an undescribed genus. These three have names as *Machaeranthera* as well as *Haplopappus*.

Sects. *Ericameria, Stenotopsis, Macronema* and *Asiris.* Nesom, *et al.* (submitted) have removed a group of species as a separate, new genus. These are primarily species of the Chihuahuan Desert, formerly recognized as *Ericameria.* Nesom (1990) has expanded the boundaries of true *Ericameria* as a genus to encompass 27 species formerly belonging to *Haplopappus* sects. *Ericameria, Macronema, Asiris* and *Stenotopsis*, making the genus coordinate in rank and variability with *Chrysothamnus*, although somewhat larger.

Sect. *Hazardia* as a separate genus (Clark 1979).

Sect. *Hesperodoria* as a separate genus (Greene 1906). As observed by Hall (1928), the two species of *Hesperodoria* are very different from each other. The single remaining species of North American *Haplopappus* without a name in a segregate genus, *Haplopappus salicinus* S.F. Blake, was based on a specimen cited by Hall as *Haplopappus* (*Hesperodoria*) *scopulorum* (M.E. Jones) H.M. Hall. This taxon apparently is still known only from the type collection, and we are not able to make a judgment on its taxonomic placement. Anderson & Weberg (1974) have suggested that it is similar to the monotypic genus *Vanclevea.*

Sect. *Isocoma* as a separate genus (Johnston 1970; Turner 1972; Nesom, in prep.).

Sect. *Isopappus* as the separate genus *Croptilon* (Smith 1965; 1981). One species, *Haplopappus occidentalis* H.M. Hall, has been segregated as the monotypic genus *Benitoa* (Keck 1956).

Sect. *Oonopsis* as a separate genus (Greene 1896).

Sect. *Oreochrysum* as a separate, monotypic genus (Rydberg 1906). Anderson & Creech (1975) have treated it as a species of *Solidago.*

Sect. *Osbertia* as a separate genus (Turner & Sundberg 1986).

Sect. *Prionopsis* as a separate genus (Nuttall 1841; Johnston 1970; Howe 1975).

Sect. *Pyrrocoma* as a separate genus (Mayes 1976).

Sect. *Stenotus* as a separate genus of six species. Greene (1894) reinstated *Stenotus* as a genus, but it has not had a modern treatment at that rank, although that of Hall (1928) remains correct in its essence. Aven Nelson added many taxa that were synonymized by Hall, but only a single additional species has been recognized since Hall's treatment (Nesom 1989).

After the consolidation of *Ericameria*, and with the recognition as genera of the other groups as noted above, 7 North American species remain to be dealt with in *Haplopappus*, all of which are in sect. *Tonestus. Tonestus* also has been regarded as a distinct genus (Nelson 1904), and except for the unusual *H. microcephalus*, there appears to be recent general agreement on the members that are included (Anderson 1980; Tiehm & Shultz 1985).

Tonestus is similar to *Stenotus* in its herbaceous habit, primarily monocephalous stems and base chromosome number of $x=9$. The overlapping nomenclatural synonyms demonstrate at least an early lack of understanding

of their relationships and the boundaries between them. Referring primarily to habit, Hall (1928: p. 39) made the claim that "The sections *Stenotus, Tonestus*, and *Macronema* form an almost continuous series," and he also placed *Oreochrysum* as a closely related element of this group. More recently, Clark, *et al.* (1980) also referred to *Stenotus* as a "woody shrub," and on the basis of similar habit and flavonoids, placed it in the same lineage as *Macronema* and *Ericameria*. Hall believed that *Stenotus* was phylogenetically connected to *Macronema* as well as *Tonestus*, but Clark, *et al.* (1980) apparently excluded *Tonestus* from a close relationship with the other two. Finally, Nesom (1989) speculated that *Tonestus* might be closely related to *Macronema* and *Stenotus*.

We observe that plants of both *Stenotus* and *Tonestus* are very different from those of the woody shrubs found in *Macronema* and *Ericameria*. The former two have woody roots and caudex branches or rhizomes, the above ground parts are distinctly herbaceous and the basal leaves are persistent. Further, studies of restriction site variation in chloroplast DNA (Morgan, unpubl.) show *Tonestus* (*T. pygmaeus*) to be in the same clade as *Solidago* (*S. altissima* L.), and *Oreochrysum* (≡*S. parryi*), most closely related to the latter and very strongly separated from the group of species that includes *Ericameria* (sensu Nesom 1990, including *Macronema*) and *Chrysothamnus*.

Stenotus was not included in Morgan's investigations of DNA restriction sites, but we do not believe that it is necessarily closely related to *Tonestus*. They appear to be distinct, unconnected groups. There are patterns of variability in each genus that are at least superficially similar, but the two can be distinguished morphologically by the features in the following key.

1. Leaves and stems eglandular (short stipitate glandular in 2 species); leaves entire, 3 nerved or when linear, 1 nerved, the cauline absent or reduced to small bracts, not clasping; heads 1 per stem; phyllaries lanceolate to obovate, strongly differentiated from the leaves, not foliaceous, with 3-5 parallel nerves ..... *Stenotus*

1′ Leaves and stems densely long stipitate glandular (eglandular in 1 species); leaves coarsely toothed (entire in 2 species), 1 or 3 nerved, the cauline well developed, usually continuing unreduced to immediately below the heads, clasping to subclasping; heads 1(-5) per stem (mostly 5-13 in 2 species); phyllaries lanceolate, the outer 1 nerved, usually foliaceous, grading into the bracteal leaves and into the inner phyllaries . *Tonestus*

The species of *Tonestus* are distinguished from *Stenotus* principally by the presence of well developed cauline leaves, 1 nerved phyllaries and usually prominently foliaceous phyllaries. Five of the species have leaves with toothed margins and almost all have a tendency to produce several headed capitulescences. Two species with entire leaves and monocephalous stems (see below) often are similar in general appearance to some species of *Stenotus*, but we

feel that these similarities reflect convergence rather than homology, because in their distinctive phyllaries, they clearly belong with *Tonestus*. Finally, *Tonestus* and *Stenotus* appear to have distinctive ecological preferences. The species of *Tonestus* mostly occur in alpine zones, where they inhabit rock outcrops, cliffs and talus, although *T. pygmaeus* and *T. lyallii* also are commonly found in rocky or gravely soil. Two species of *Tonestus*, *T. graniticus* and *T. microcephalus*, occur at lower altitudes. The species of *Stenotus* generally grow below alpine altitudes, characteristically with sagebrush (although sometimes reaching alpine habitats) and they occur mostly in rocky or gravely soil.

To complete the reinstatement of *Tonestus*, we provide a taxonomic summary of the genus with the necessary nomenclatural transfers. This also completes the apportionment of North American *Haplopappus* sensu Hall among its natural segregate genera, except for the problems noted above with the three species of sect. *Blepharodon* sensu Hall and with *H. salicinus*.

Tonestus A. Nelson, Bot. Gaz. (Crawfordsville) 37:262. 1904. *Haplopappus* sect. *Tonestus* (A. Nelson) H.M. Hall, Carnegie Inst. Washington Publ. 389:34. 1928. Type species: *T. lyallii* (A. Gray) A. Nelson

Herbaceous perennials with branched caudices or stout rhizomes, often from a thick taproot, with stems and leaves densely stipitate glandular, eglandular in 2 species. Leaves usually with at least a few coarse teeth, entire in 3 species, the basal persistent, the cauline little reduced upward, the upper clasping to subclasping or not clasping. Heads mostly campanulate, usually solitary, sometimes 2-5 per stem in a loose corymb or in 2 species 5-15; phyllaries lanceolate, 1 nerved, in 3-4 nearly equal series or 5-7 graduated series, the outer foliaceous, often grading into the upper leaves and into the more chartaceous inner phyllaries (not foliaceous in 2 species); receptacles shallowly convex, naked. Ray flowers present or absent, pistillate, fertile, the corollas yellow, prominent. Disc flowers perfect, fertile, the corollas yellow, tubular, slightly ampliate upward; style branch appendages mostly acute, about equal in length to the stigmatic portions, with collecting appendages with short hairs or merely papillate. Achenes narrowly oblong, compressed or slightly fusiform to subcylindric, densely to sparsely strigose sericeous; pappus of numerous barbellate bristles in a single series. Base chromosome number, $x=9$ (Anderson 1980; Tiehm & Shultz 1985; Spellenberg 1986).

1. **Tonestus aberrans** (A. Nelson) Nesom & Morgan, *comb. nov.* BASIONYM: *Macronema aberrans* A. Nelson, Bot. Gaz. (Crawfordsville) 53:226. 1912. *Haplopappus aberrans* (A. Nelson) H.M. Hall, Carnegie Inst. Washington Publ. 389:185. 1928.

2. **Tonestus alpinus** (L. Anderson & S. Goodrich) Nesom & Morgan, *comb. nov.* BASIONYM: *Haplopappus alpinus* L. Anderson & S. Goodrich, Great Basin Nat. 40:73. 1980.

3. *Tonestus eximius* (H.M. Hall) A. Nelson & Macbr., Bot. Gaz. (Crawfordsville) 65:70. 1918. BASIONYM: *Haplopappus eximius* H.M. Hall, Univ. Calif. Publ. Bot. 6:170. 1915.

4. **Tonestus graniticus** (Tiehm & L. Shultz) Nesom & Morgan, *comb. nov.* BASIONYM: *Haplopappus graniticus* Tiehm & L. Shultz, Brittonia 37:165. 1985.

5. *Tonestus lyallii* (A. Gray) A. Nelson, Bot. Gaz. (Crawfordsville) 37:262. 1904. BASIONYM: *Haplopappus lyallii* A. Gray, Proc. Acad. Nat. Sci. Philadelphia 1863:64. 1864. ~~*Tonestus lyallii*~~ (A. Gray) J.T. Howell, *Fl. N.W. Amer.* 300. 1900.

6. **Tonestus microcephalus** (Cronq.) Nesom & Morgan, *comb. nov.* BASIONYM: *Haplopappus microcephalus* Cronq., Madroño 11:186. 1951.

7. **Tonestus peirsonii** (Keck) Nesom & Morgan, *comb. nov.* BASIONYM: *Haplopappus eximius* subsp. *peirsonii* Keck, Madroño 5:169. 1940. *Haplopappus peirsonii* (Keck) J.T. Howell, Leafl. W. Bot. 6:86. 1950.

8. *Tonestus pygmaeus* (Torr. & Gray) A. Nelson, Bot. Gaz. (Crawfordsville) 37:262. 1904. BASIONYM: *Stenotus pygmaeus* Torr. & Gray, *Fl. N. Amer.* 2:237. 1842. *Haplopappus pygmaeus* (Torr. & Gray) A. Gray, Amer. J. Sci., ser. 2, 33:239. 1862. *Macronema pygmaeum* E. Greene, Erythea 2:73. 1894.

The species of *Tonestus* can be divided into four intergrading morphological groups: (1) *T. aberrans* and *T. graniticus* with toothed leaves and phyllaries in 5-7 graduated series; the latter is unusual in its reduced cauline leaves and numerous, campanulate-turbinate heads lacking prominently foliaceous outer phyllaries; (2) *T. alpinus, T. eximius* and *T. peirsonii* with toothed leaves and phyllaries in 3-4 nearly equal series; (3) *T. lyallii* and *T. pygmaeus* with entire leaves and phyllaries in 3-4 nearly equal series; the latter is the only species in the genus with an eglandular vestiture; and (4) *T. microcephalus* with entire leaves, heads in definite corymbs and phyllaries not foliaceous but with prominent, herbaceous apical extensions. In these characteristics, *T. microcephalus* is a somewhat aberrant species in the genus, but in its cliffside habitat, stout caudex branches, densely leafy stems and 1 nerved phyllaries, it is best placed in *Tonestus*. In this light, the herbaceous apical extensions of the involucral bracts should prove to be homologous with the foliaceous outer bracts that are characteristic of most of the rest of the genus. *Tonestus graniticus*, which is more securely placed as a species of *Tonestus*, also has differentiated, non foliaceous bracts and corymboid heads and it also occurs in habitats below alpine zones.

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